A PRELIMINARY INVESTIGATION INTO THE INFLUENCE OF TURBULENCE ON LARVAL FEEDING IN TWO SPECIES OF BLACKFLY, *SIMULIUM CHUTTERI* LEWIS AND *SIMULIUM NIGRITARSE* COQUILLETT (DIPTERA, SIMULIIDAE), FROM THE GREAT FISH RIVER, SOUTH AFRICA

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ABSTRACT

Since 1977, larvae of the pest species *Simulium chutteri* Lewis have largely replaced *Simulium nigritarse* Coquillett as the dominant species of blackfly in the Great Fish River in the eastern Cape. This is thought to be due to a change from intermittent to continuous water flow, since the completion of an interbasin water transfer scheme from the Orange River to the Great Fish River. Changes in turbulence of the flow may be one of the factors responsible for this shift in species composition, and in this study, the effect of turbulence on the feeding of larvae was investigated under laboratory conditions. Turbulence was measured as Reynold's number, with larvae feeding on algae under different conditions of turbulence created in glass tubes. Feeding activity was measured by measuring algal (*Chlorella*) cell counts and chlorophyll *a* concentrations from gut contents after feeding, and by cephalic fan activity. The results indicate that, under conditions of higher turbulence, *S. chutteri* feeds more efficiently than does *S. nigritarse.*

Keywords: blackfly larvae, turbulence, flow rates, Reynold's number, feeding behaviour

INTRODUCTION

Simulium chutteri Lewis is well known in its adult stage as a pest, as the females imbibe blood from livestock (Chutter 1968). Car & de Moor (1984) quote farmers reporting losses in stock production and occasional deaths in young animals through excessive blood feeding by this species. Studies by Chutter (1972) and Scott et al. (1972) showed that between 1970 to 1971, *Simulium nigritarse* Coquillett and *Simulium adersi* Pomeroy were the dominant blackfly species in the Great Fish River at Carlisle Bridge (33°04'55"S 26°13' 45"E), although *S. chutteri* was present in low numbers (O'Keeffe & de Moor 1988). Since 1977, the Great Fish River and its surroundings (Fig. 1) have been plagued by increasing numbers of *S. chutteri*, which replaced *S. nigritarse* and *S. adersi* as the dominant blackfly species (de Moor & O'Keeffe 1987). The change in species composition occurred after the completion (in 1977) of an interbasin transfer scheme whereby water was channelled from the Orange River to the Great Fish River. The water transfer resulted in a change in the Great Fish River from intermittent flow to perennial flow (O'Keeffe & de Moor 1988).

A similar change in species composition has been reported with damming of rivers in northern Alberta and Saskatchewan, whereby *Simulium luggeri* Nicholson and Mickel replaced *Simulium articum* Malloch as the dominant species, after changes in flow regimes, following impoundment (Wood 1985). Coetzee (1982) found that in the upper reaches of the Great Fish River, upstream of the outlet of Orange River water, *S. nigritarse* larvae were still more abundant than those of *S. chutteri.* An unpublished survey carried out by the author and colleagues during 1985 indicated that *S. nigritarse* was a dominant macroinvertebrate species in the upper reaches of the Great Fish River. Although regulated by numerous small farm dams, the flow in these reaches continued to be seasonal. More recent observations (pers. obs. and communication from local farmers) indicate that water in these reaches remains clear for most of the year. Conditions may, however, become turbid during spates after rainfall. The water in the lower reaches is generally more turbid. O'Keeffe & de Moor (1988) investigated flow patterns and water chemistry for the Great Fish River, both upstream and downstream of the outlet, prior to, and after, the introduction of Orange River water. They found that there had been marked changes in flow regimes and water chemistry below the outlet, compared to the situation prior to the introduction of Orange River water.

Downstream of the Orange River water outlet, relative abundances of both *S. nigritarse* and *S. adersi* declined, while those of *S. chutteri* increased greatly subsequent to the inflow of Orange River water (O'Keeffe & de Moor 1988). Current velocity and water volume are known to be important in controlling habitat suitability for various *Simulium* species (de Moor 1994). *S. chutteri* is normally found in fast-flowing, large rivers, while *S. nigritarse* and *S. adersi* are generally found in small streams to medium sized rivers (de Moor 1989; Palmer & de Moor 1998). Palmer & de Moor (1998) have also indicated that, although *S. chutteri* has been recorded in low numbers from several small, clear rivers in the eastern Cape, it only achieves high

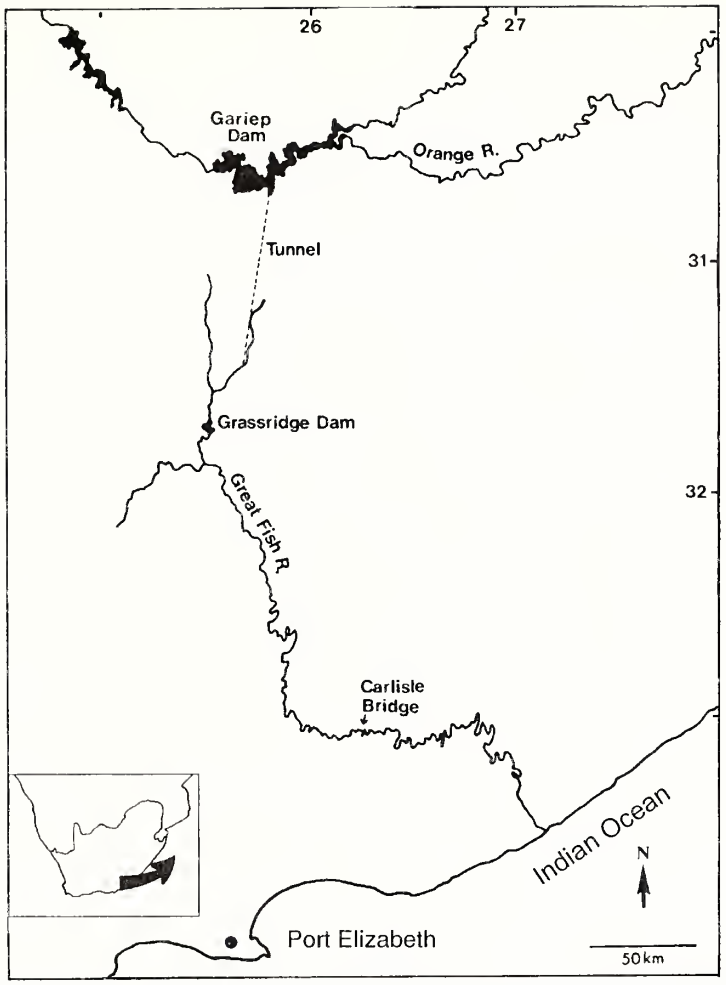

Fig. 1: The Great Fish River, indicating the position of Carsile Bridge. The dashed line represents the tunnel connecting the Orange and Great Fish river systems.

population densities in large, turbid rivers, such as the Vaal River. During a period of low flow following a severe drought (from 1980-1982), when the turbidity in the lower Vaal river was noted to be unusually low, the normally-dominant simuliid species, *S. chutteri*, was replaced by *S. hargreavesi* (Car & de Moor 1984; de Moor 1994). The avoidance of clear water by *S. chutteri* is further confirmed by the observation by Palmer & O'Keeffe (1990) that numbers of *S. chutteri* drop significantly downstream of impoundments where clearer water is released into normally-turbid rivers.

The effect of changing flow conditions on feeding activity has been documented for several simuliid species. For example, distinct differences in fan adduction activity relating to increased current speed have been shown for nine European *Simulium* species (Schröder 1980, 1988). Studies on feeding behaviour, rates of ingestion and selectivity of food particle size have also been carried out for several Nearctic species, for example, Kurtak (1978), Craig & Chance (1982), Ciborowski & Craig (1989), Hart & Latta (1986), Hart et al. (1991). For this study, laboratory experiments were set up to investigate the effects of increasing turbulence, defined by Reynolds number, on the feeding ability of *S. chutteri* and *S. nigritarse*.

MATERIALS AND METHODS

The calculation of Reynold's number

Reynolds number is the ratio of inertial forces to viscous forces in liquids (Smith 1975; Vogel 1981) and defines the properties of fluid motion. Low Reynolds numbers (below 500) indicate laminar flow, while Reynolds numbers approaching 2000 or more indicate turbulent flow.

Reynold's number (*Re*) is calculated according to the equation:

$$Re = \frac{Ul\,\rho}{\mu} = \frac{Ul}{\upsilon}$$

where:
U is the mean velocity (cm s^{-1})
l is the tube diameter (cm)
ρ is the density of water at a specified temperature
μ is the dynamic viscosity of water
υ is the kinematic viscosity of water

Collection of samples and measurement of larvae

Larvae were collected from the Great Fish River at Carlisle Bridge (Fig. 1), during late May (winter) and again in late October into early November (summer) for both species. As it was not possible to do all the experiments at the same time, summer populations of larvae of both species were used for the haemocytometer-analysed results and for fan adduction counts, while winter populations were used for those analysed by fluorometry (see analysis of feeding below). As final instar larvae do not feed (de Moor 1982a), sixth instar larvae were selected for all experiments. These differ from final instar larvae in that the respiratory histoblasts are not yet fully developed and the cervical sclerites are not yet fully separated from the preocciput (de Moor 1982 c & b). Recently-moulted larvae (those with pale yellow head capsules) were used, as the rate of feeding may differ in older larvae of the same instar (de Moor 1982b). Larvae of each species from both populations were measured to compare sizes, in case one group should be bigger than the other, which could also influence feeding. The total body lengths of 75 typical sixth instar larvae of each species were measured using a dissecting microscope with a graticule. Differences in winter and summer populations have been previously documented (de Moor 1982a, 1982b), and can be explained in terms of reduced water temperatures resulting in slower growth rates, longer development periods and, hence, the development of larger larvae. No attempts were made to investigate sexual difference between larvae in these experiments, and although de Moor (1982a) found that females of later stage larvae were larger than the equivalent males, Elsen et al. (1978) have indicated that sex has no influence on larval feeding in *S. damnosum*.

Acclimatization

Before initiating the experiment, the larval alimentary tracts had to be cleared of food. A section of plastic guttering, connected to a water inlet at one end and with an outlet at the other end (Fig. 2), was set up as a channel to allow gut clearance. A continual flow of clean water could pass through this channel when required. Strips of hard, clear plastic measuring 5 mm by 100 mm, with cotton loops at each end, were suspended lengthwise down the channel, into the flowing water, from wooden rods, which rested across the channel (Fig. 3). Larvae collected from the field were placed in the channel, and some of the larvae attached themselves to these plastic strips, which would later be transferred, bearing larvae, into the experimental tubes. The larvae were retained in the channel in algae-free water to clear their alimentary tracts before starting the feeding experiments. The gut retention time for *Simulium* species has been shown to be highly variable, ranging from 0.5

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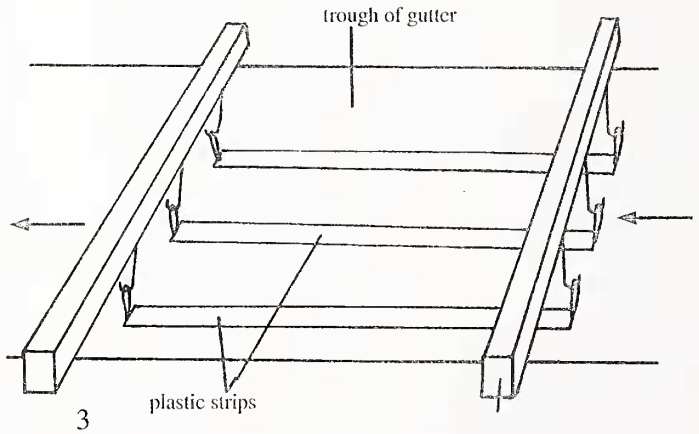

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Figs 2 & 3. Apparatus used for gut clearance of blackfly larvae. **2**, photograph of the apparatus showing diagonal bars from which plastic strips were suspended. **3**, Diagrammatic representation of a section of the rigid plastic strips on which larvae settled. Arrows indicate the direction of water flow.

hours to 4 hours (Kurtak 1978; Ladle & Hansford 1981; Fredeen 1964; Chance 1970). Preliminary investigations were carried out to establish the required clearance times for *S. chutteri* and *S. nigritarse*. This was done by removing larvae from the channel every 30 minutes and investigating the contents of the alimentary tracts on a slide under a microscope. These tests revealed that 2 hours was a sufficient time period for gut clearance in both *S. chutteri* and *S. nigritarse*. Quantitative measurements were not done for this.

The larvae used for these experiments were acclimatized to 21°C in the laboratory, irrespective of season collected, and the water temperature in the experimental tank was maintained at 21°C. Winter water temperatures would have been cooler, but it was decided to approximate summer temperatures for the experiments as feeding may have been reduced and would, therefore, be harder to measure at lower water temperatures.

Apparatus and Experimental Procedure

The experimental apparatus for this investigation was modified after Noble (1970). It consisted of a glass tank with a capacity of 15*l*, filled with a suspension of *Chlorella*, in which a system of interlocking, open-ended glass tubes (Figs 4 & 5A) was submerged. The upper tube was wider (internal diameter 25 mm) than the lower tube (internal diameter 10 mm), since tubes with smaller diameters produce more turbulent conditions.

The upper tube was attached to a water pump, which could be adjusted to vary flow rates. The flow of water from the pump through the tubes was controlled using a rheostat. Velocities at different rheostat settings were determined by introducing drops of 1.25M potassium permanganate solution (used as an indicator dye) through a port on the upper side of the tube near the mouth (Fig. 5A), into the middle of the stream of water passing through the tube. The nucleus of the droplet moved forward, with a thin trace of colour trailing behind. The progress of the droplet was timed over a fixed distance. This was repeated twenty times for each rheostat setting to estimate the velocity so that Reynold's number could be calculated.

Laboratory tests involved a three-step process: field collection and measurement of larvae; laboratory acclimatization, and feeding experiments.

Feeding tests

After clearing the alimentary tracts of food imbibed in the natural river environment (as described above), the plastic strips, bearing larvae, were carefully transferred to the centre of one of the glass tubes in the tank (Fig. 4). The strips were positioned longitudinally down the center of a tube and attached by the cotton loops to hooks within the tube (Fig. 5B). In this way, different groups of larvae could be subjected to one of six different conditions of turbulence (i.e. six values for Reynold's number). A maximum of about 10 larvae were introduced to a tube each time, since it was found that, at higher densities, feeding of individual larvae was often interrupted by movements of neighbouring larvae.

Once the larvae had settled in the tubes (2 minutes acclimatization allowed each time), the flow

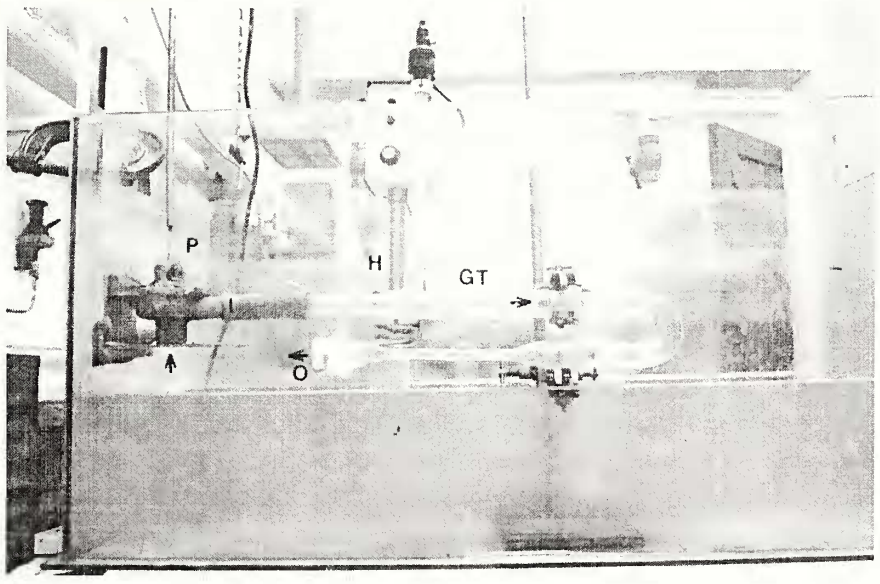

Fig. 4: The experimental apparatus within an aquarium (with water level lowered to show inner apparatus more clearly) showing tubes in which turbulence can be varied. LEGEND: GT = glass tubes; H = heat stirrer; I = inlet; O = outlet; P = part of pump.

was switched on, creating the required level of turbulence. Feeding was allowed to continue for 10 minutes before switching off the flow and removing the larvae from the tube. Larvae were placed in labelled vials containing 5% formalin, or in cold insect saline, and immediately refrigerated, depending on the subsequent method of analysis of algal content (see below for a description of these methods).

Oxygen concentration of the water in the tank was frequently determined using the Winkler method, to confirm that it was never in short supply. Because the water was rich in algae, Alsterberg's modification of the Winkler titration for water rich in organic matter was used (in Mackereth et al. 1978).

ANALYSIS OF FEEDING

Three methods were used to compare feeding in the two species. Larval gut contents (equivalent to the amount of algae ingested) were estimated using haemocytometer counts of algal cells, and fluorometric measurements of chlorophyll *a*. A third estimate involved counting the number of adductions of a blackfly's cephalic fans over a fixed period of time, to see if the behavioural response was affected by changing turbulence.

Haemocytometer analysis

After feeding, the larvae were immediately preserved in 5% formalin for later dissection.

The entire gut content of a larva was dissected and dispersed in 1.00 ml of distilled water and subsamples of this were examined under a Neubauer Bright Line Haemocytometer. The haemocytometer was standardized to hold exactly 0.0009 ml of sample, and all of the algal cells present in this volume were counted. Five separate counts of algal cells were recorded for each 1 ml sample (i.e. for each larva), and this was done for the gut contents of 15 larvae at each of the six levels of turbulence (*Re* values). The mean number of cells per 0.0009 ml sample from the gut contents was taken to represent the amount ingested for each larva, and these values were compared for the two species. Comparisons between the feeding of the two species was done using a t-test at each level of turbulence.

A control experiment was run to see if the same quantities and size ranges of cells were available to both species. Algal cell counts and size measurements were done on water samples taken directly from the 15*l* tank prior to each set of experiments. Comparisons of the size of algae in the tank to the size ingested by the larvae of each species were analysed using t-tests.

Fluorometry analysis

Immediately after feeding, larvae were placed in a vial containing cold insect saline and refrigerated at 4°C. Refrigeration was chosen rather than storage in a preservative so that the chlorophyll *a*

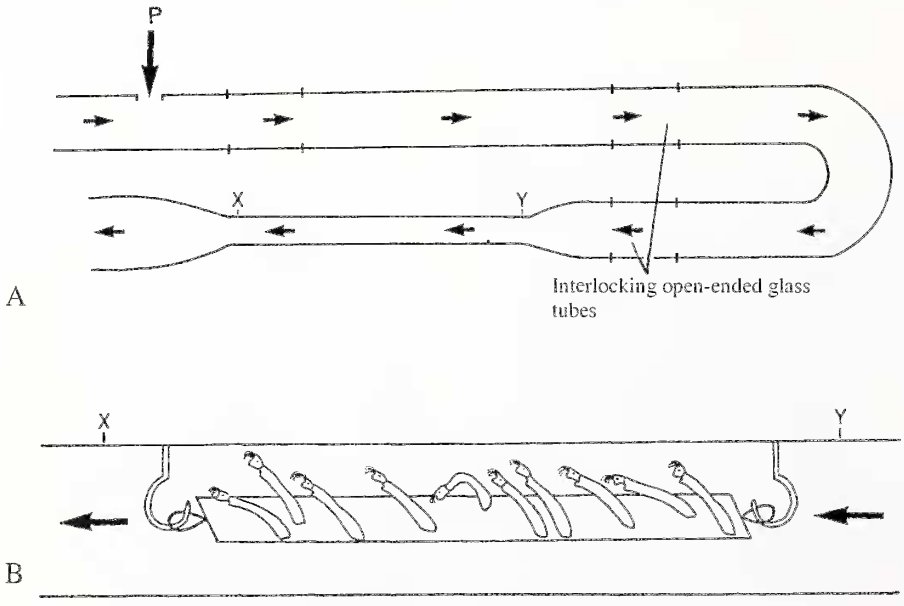

Fig. 5. A. Diagrammatic representation of interlocking, open-ended glass tubes used to measure turbulence. Drops of potassium permanganate are introduced through a small aperture (P) to estimate current speeds (and hence, turbulence). **B**. Detail of section X-Y (from A) illustrating larvae resting on plastic strips. Arrows indicate direction of water flow.

would not be chemically altered. Dissection was undertaken as soon as possible thereafter. Alimentary tracts were dissected from ten larvae for each of the six turbulence levels, gut contents were then pooled from each group of ten and placed in a vial containing 10 ml of 90% acetone. This was carried out three times for each of the six turbulence levels. Chlorophyll *a* concentration was measured using a Turner Fluorometer model 111. This was set at its greatest sensitivity and calibrated using standard chlorophyll *a* of known concentrations and 90% acetone as a blank. The feeding of the two species at different turbulence levels was compared using a t-test.

A control test of the chlorophyll *a* concentration of the water in the tank was measured at the onset of each set of experiments to check that conditions remained constant.

Observations of cephalic fan adductions

In blackfly larvae, particles from flowing water are trapped in the cephalic fans and transferred to the mouth by means of fan adductions, combined with a series of movements of other mouthparts. Fan adduction rate therefore gives an indication of the feeding rate (Craig 1977; Craig & Chance 1982; Hart & Latta 1986; Currie & Craig 1987; Palmer & Craig 2000). The number of cephalic fan adductions per minute were noted for three individual larvae at each value of Reynold's number for both *S. chutteri* and *S. nigritarse*. Craig & Chance (1982) found that only the primary fans of simuliids are directly involved with capturing particles from the water, and only these fans were observed.

While the animals were in the experimental tubes, each individual was observed three times, for a minute each time. A dissecting microscope was set up against the tank to facilitate observations. The contractions of only one fan were counted for each larva. Comparisons between the fan adduction rates of the two species was done using a t-test for each turbulence level.

RESULTS

Length measurements

Body length measurements of 75 larvae at the chosen stage of development (sixth instar) show that there were no significant differences between the sizes of larvae within each species ($p<0.05$), and that the sixth instar larvae of the two species had a similar size range. The winter populations of both species were, however, significantly ($p<0.005$) larger than the summer populations. Information on the sizes of larvae in the two populations is given below.

SUMMER POPULATIONS

S. chutteri

range = 3.15-4.35 mm; mean = 3.65 mm ± 0.34.

S. nigritarse

range = 3.22-4.04 mm; mean = 3.58 ± 0.03.

WINTER POPULATIONS

S. chutteri

range= 4.72-6.20 mm; mean = 5.36 ± 0.43.

S. nigritarse

range = 4.49-6.15 mm; mean = 5.27 ± 0.52.

Feeding experiments

Measurements of algal cell sizes revealed that similar sized cells were available in the experimental tank for both species at the onset of experiments using haemocytometer measurements (Table 1). Wotton (1973) found a significant positive correlation between particle sizes in simuliid guts and in stream water, showing feeding to be unselective, and Chance (1970), despite finding selective feeding in the laboratory, found that in the field, feeding was unselective. For both *S. chutteri* and *S. nigritarse,* the mean size of the cells ingested was, however, found to be smaller than the mean size of the cells available, indicating that both species selectively ingested a slightly smaller range of cells sizes than the mean range available (Tables 1 & 2).

A 10-minute feeding period was found to be long enough to allow a measurable amount of ingestion. Haemocytometric analysis of the gut contents of larvae which fed under different conditions of

Table 1. Size ranges of algal cells available in tank prior to feeding experiment. Standard deviations are indicated in parenthesis (n = 35)

	Size range (µm)	Mean (µm)
S. chutteri	200-1300 (260)	683
S. nigritarse	230-1100 (220)	550

Table 2. Size ranges of algal cells ingested at each turbulence level (Reynold's number) for the haemocytometry experiments. Standard deviations indicated in parenthesis (n = 15)

Turbulence (*Re*)	*S. chutteri*		*S. nigritarse*	
	Range ingested (µm)	Mean (µm)	Range ingested (µm)	Mean (µm)
174	230-1224 (245)	474	230-816 (183)	447
481	204-1097 (292)	592	230-1020 (229)	492
752	230-1020 (193)	415	230-1071 (260)	442
1487	230-995 (196)	413	230-1020 (223)	473
1638	230-893 (201)	459	230-1097 (256)	502
2004	240-836 (188)	408	230-791 (185)	451

turbulence showed a significant increase in the number of cells ingested by *S. chutteri* at higher turbulences (*Re* values of 1638 & 2004). The opposite was seen for *S. nigritarse*, with a decrease in numbers of cells ingested at higher turbulences (Fig. 6A). Comparing the two species using t-tests, highly significant differences at various turbulence levels (at *Re* values of 481, 752, 1487, 1638 and 2004: $p<0.005$) were observed, while only at Re values of 174 were cell counts not significantly different ($p>0.2$) (Fig. 6A).

For the fluorometric experiments, chlorophyll *a* concentrations in the tank were similar at the onset of experiments with each species (35.9 µg/l in the '*S. chutteri*' tank; 36.3 µg/l in the '*S. nigritarse*' tank). The results from these analyses showed a similar trend to the haemocytometer-measured experiments, but the distinction was less clear (Fig. 6B), and at a turbulence of 1487 *Re*, algal ingestion by *S. nigritarse* actually increased, as opposed to the dramatic drop observed in the haemocytometer counts. A significant difference ($p<0.05$) in chlorophyll *a* levels determined from the gut contents of each species was seen at each turbulence level, although this was greatest at the highest turbulence (*Re*=2004).

Although fan adductions ceased at turbulence values of 2004 *Re* for *S. nigritarse* (Fig. 6C), chlorophyll *a* was measured from the guts of the larvae subjected to this level of turbulence (Fig. 6B). It is possible that some algae were ingested during the 2-minute acclimation period prior to the onset of the experiments. This was not taken into consideration, and was assumed to be the same for all larvae, since they were subjected to similar conditions. Fan adduction observations showed that *S. chutteri* had a higher adduction rate than *S. nigritarse* for all turbulence levels, but this became more pronounced at higher turbulences (Fig. 6C). Significant differences ($p<0.005$) in fan adductions between the two species were observed at all but the lowest turbulences (*Re*=174). In moderately turbulent conditions (*Re*=2004), or conditions approaching high turbulence (*Re*=752, 1487 & 1638), the rhythmic fan adductions of *S. nigritarse*, which characterized feeding at lower turbulences (*Re*=174 & 481), became less regular. The fans of many individuals remained closed throughout the runs at the highest turbulences (*Re*=2004), or flicked quickly without opening properly. Others seemed unable to adduct their fans, which remained continually open. In *S. chutteri* the adduction pattern was little affected by increasing turbulence. These observations suggest that under high turbulent conditions, larvae of *S. nigritarse* were unable to feed properly.

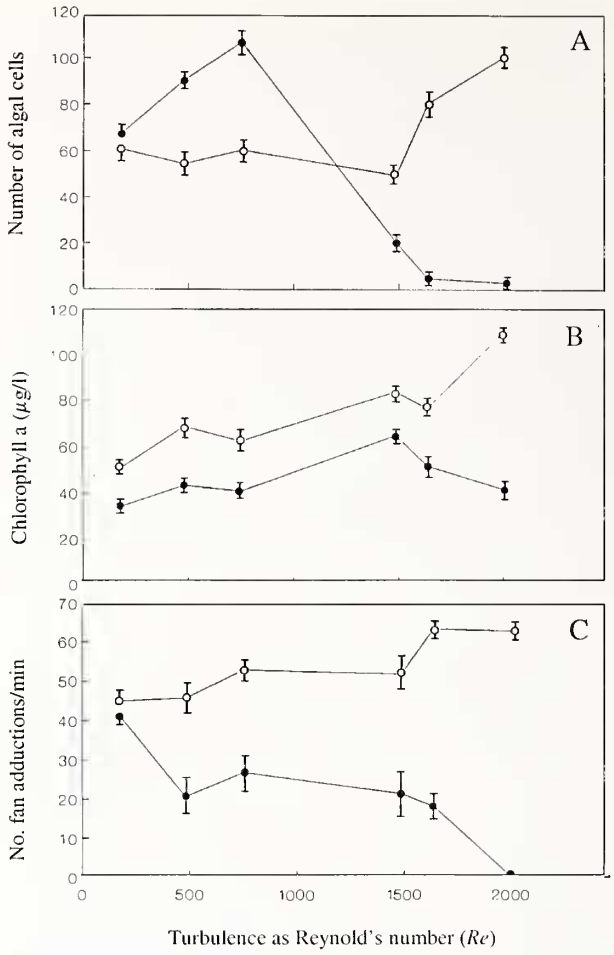

Fig. 6. Results of feeding experiments: (a) Relative numbers of algal eells eounted from the gut contents of simuliid larvae; n=10.. (b) Levels of chlorophyll *a* measured from the gut contents of simuliid larvae; n=30. (e) Fan adduetion rates per minute for simuliid larvae; n=3. Larvae were subjected to flow eonditions of increasing turbulence (*Re* values). Standard errors are indicated by vertieal lines. ○=*S. chutteri;* ● *S =nigritarse.*

DISCUSSION

A potential problem with interpreting the data obtained during these experiments is that the larvae in the experimental tubes may be responding directly to changes in current velocity rather than to the changes in turbulence. However, since the calculation of Reynold's number takes current velocity into account, the responses measured are in relation to Reynold's number and therefore assumed to be due to changes in turbulence. Another limitation of this experimental work is that higher turbulences, above *Re* values of 2004, could not be attained with the apparatus used. This means that most of the studies fell into the flow range that is transitional between laminar and turbulent flows. In the field, the natural turbulence would be much higher than that measured in these experiments. Finally, an increased number of replicates would have provided better confidence in the statistical analysis, but the time limitations of the project did

not allow this. Despite these shortcomings, the different responses of the two species to changes in turbulence was clearly demonstrated using three different methods. It is recommended that further work be done on the feeding of these two species to corroborate these results.

A number of conditions besides turbulence have changed in the Fish River since 1977, all of which may have influenced the invertebrate community, and which may have played a part in the observed change in species dominance. There have been changes in water chemistry (O'Keeffe & de Moor 1988) and the high turbidity and strong flow conditions associated with high numbers of *S. chutteri* larvae (de Moor 1994) now prevail in the Great Fish River. Certain behavioural responses such as oviposition are known to affect the success of simuliids. de Moor et al. (1986) found that females of *S. chutteri* scatter eggs in slower-flowing water upstream of rapids. The small larvae colonize the slower flowing reaches, while the more mature larvae drift and establish themselves in the rapids, unlike the coexisting species, *S. nigritarse* and *S. adersi,* which restrict themselves to the slower flowing reaches of the river. *Simulium nigritarse* lays its eggs in patches below the water surface on partly submerged stones (Chutter 1972). Oviposition and larval establishment are therefore aspects of the life history of these species that are directly affected by flow.

CONCLUSIONS

Although other factors may influence the invertebrate population structure, the results of this study do indicate that turbulence is one of the factors favouring the change in simuliid species composition in the Great Fish River. After quantifying the effects of increased turbulence on the feeding of *S. chutteri* and *S. nigritarse*, it is not surprising that changes in the community structure have occurred, favouring the pest species *S. chutteri*.

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